Diurnal fluctuations in seawater pH influence the response of a calcifying macroalga to ocean acidification

Christopher E. Cornwall1,†, Christopher D. Hepburn2, Christina M. McGraw3,5, Kim I. Currie4, Conrad A. Pilditch6, Keith A. Hunter3, Philip W. Boyd4,† and Catriona L. Hurd1,†

1Department of Botany, 2Department of Marine Sciences, 3Department of Chemistry, and 4National Institute for Water and Atmospheric Research Ltd (NIWA), Centre for Physical and Chemical Oceanography, University of Otago, PO Box 56, Dunedin, New Zealand
3School of Chemistry and Biochemistry, University of Clark, 950 Main Street, Worcester, MA, USA
6School of Biological Sciences, University of Waikato, Private Bag 3105, Hamilton, New Zealand

Coastal ecosystems that are characterized by kelp forests encounter daily pH fluctuations, driven by photosynthesis and respiration, which are larger than pH changes owing to ocean acidification (OA) projected for surface ocean waters by 2100. We investigated whether mimicry of biologically mediated diurnal shifts in pH—based for the first time on pH time-series measurements within a kelp forest—would offset or amplify the negative effects of OA on calcifiers. In a 40-day laboratory experiment, the calcifying coralline macroalga, Arthrocardia corymbosa, was exposed to two mean pH treatments (8.05 or 7.65). For each mean, two experimental pH manipulations were applied. In one treatment, pH was held constant. In the second treatment, pH was manipulated around the mean (as a step-function), 0.4 pH units higher during daylight and 0.4 units lower during darkness to approximate diurnal fluctuations in a kelp forest. In all cases, growth rates were lower at a reduced mean pH, and fluctuations in pH acted additively to further reduce growth. Photosynthesis, recruitment and elemental composition did not change with pH, but δ13C increased at lower mean pH. Including environmental heterogeneity in experimental design will assist with a more accurate assessment of the responses of calcifiers to OA.

1. Introduction

Ocean acidification (OA), the process of sustained absorption of anthropogenically derived atmospheric CO2 by the world’s oceans [1], is predicted to cause large-scale changes in many marine ecosystems [2]. This absorption of CO2 has already led to significant changes to the seawater carbonate system and is predicted to cause a decrease in pH of 0.3–0.5 units by the end of the century [3]. If pH is reduced by 0.4 units, these changes are expected to reduce [CO32-] by 30%, increase [HCO3-] by 9% and increase [H+] by approximately 200% [3,4]. OA is also predicted to decrease the net calcification and/or increase dissolution of many organisms that build CaCO3 structures [5].

In the open ocean, pH does not vary greatly in time and space, making laboratory simulations of future pH levels relatively straight forward [6]. By contrast, near-shore marine organisms live in a highly variable pH environment where daily pH fluctuations owing to biological activity can exceed 1 unit [6–16]. These changes are often driven by primary producers increasing pH in the surrounding seawater during the day via photosynthesis, and decreasing pH at night owing to respiration [15]. In some regions, night-time decreases in pH (to less than 7.4; [17]) exceed those predicted owing to OA over the next 100 years (pH ~ 7.65; [3]).

Currently, it is not known how daily shifts in pH within near-shore ecosystems influence the physiology or the ecology of calcifying organisms, nor is it understood how these pH fluctuations could interact with the effects of OA.
It is difficult to reproduce the environmental heterogeneity that occurs in the field within a laboratory setting. For example, experimental manipulations of light and temperature in experiments with marine species usually use tightly controlled continuous levels, even though these environmental factors are much more variable in the field [18,19]. To date, only one study has manipulated pH over a diurnal cycle mimicking ecologically relevant pH shifts (daytime \( \text{pH} = 8.00 \), night-time \( \text{pH} = 7.77 \)) to examine short-term (3–6 day) effects on coral recruits [20]. Although this study [20] did not report the pH variability occurring naturally in the organism’s habitat, they found that in some instances coral recruits responded positively to both daily fluctuations in pH and to OA. Incorporating such daily fluctuations in pH/CO₂ into OA manipulation studies is the next step in better identification of the responses of near-shore species to climate change-mediated alteration of pH conditions.

Periods of high pH/low CO₂ could potentially ameliorate some of the negative effects of OA on calcifying organisms [12,15,20], by providing them with a period of respite where they can calcify at much higher rates [9]. This study investigated the interactive effects of daily fluctuations in pH that simulate biological activity, and the long-term decline in seawater pH predicted owing to OA on the growth and physiology of the coralline macroalga Arthrocardia corymbosa, a member of a genus that is found in temperate regions of both the Northern and Southern Hemispheres [21,22]. Arthrocardia corymbosa was incubated in pH treatments representative of typical surface seawater today and seawater pH predicted for 2100 in static conditions that are characteristic of oceanic waters. Both of these treatments also included diurnal fluctuations in pH that more accurately mimicked the amplitude of pH change typical of coastal waters dominated by macroalgae than previous research investigating the effects of OA on marine organisms. The magnitude of pH change within incubations was based on pH changes measured in situ in a kelp forest (from where A. corymbosa was collected) and from published oceanic measurements [6,23]. The aim of the laboratory incubations was to determine whether elevated daytime pH (similar to that observed in regions influenced by macroalgal photosynthesis) could provide a period where high calcification rates could compensate for the overall decline predicted to occur because of lowering seawater pH owing to OA.

2. Material and methods

(a) Monitoring in situ pH fluctuations

An Envco pHEmption combined pH and temperature logger and was placed within a Macrocystis pyrifera forest (1.2 m depth) at Karitane, near Dunedin, South Island, New Zealand (45°38’20”S, 170°40’15”E) for 4–5 days in each season between 4 April 2010 and 27 May 2011. For a description of the macroalgal community composition and underwater irradiance at the study site, see Hepburn et al. [24]. pH was measured on the total scale (pHT).

(b) Macroalgal collection

Thirty assemblages of the articulate coralline alga A. corymbosa were collected on 13 March 2011 from the same M. pyrifera forest in which the coastal pH data were recorded. Each assemblage contained 10 individual A. corymbosa (40 mm high) on a small base of crustose coralline algae. Six of these assemblages were sacrificed to assess the physiological status of the macroalgae at the start of the experiment (hereafter, ‘initial’ samples).

(c) Experimental design and seawater carbonate chemistry

The remaining 24 assemblages were placed into one of four pH treatments for 40 days. pH treatment levels were multifactorial with two mean pH levels measured on the total scale (pHT 8.05 and 7.65). For each level of mean pH, there were two levels of pH variability. In one treatment, pH was held constant. In a second treatment, pH fluctuated around the mean and was 0.4 pH units higher than the mean during the day and 0.4 units lower than the mean during the night. The target mean pH within each treatment was achieved using a modified version of the pH-controlled automated culture system described by McGraw et al. [25], in which pH is measured spectrophotometrically to ±0.01 units accuracy and controlled within 0.03 units. The mean pH in the ambient seawater treatments (8.05) was selected to represent unmodified seawater from an oceanic site 68.5 km offshore (8.05) [23], a value that is very similar to that considered representative of the global mean pH of surface waters in the best practice guide (8.065) [5].

Seawater (salinity 34.5, pHT 8.05) was collected from Otago Harbour, South Island, New Zealand (45°52.51’S, 170°30.9’E) every 6 days and stored in a 1000 l tank. Mean nitrate and phosphate concentrations were 1.16 ± 0.07 and 0.24 ± 0.01 μmol l⁻¹, respectively, throughout the experiment (see the electronic supplementary materials for methodological details). Twice a day, a 1501 storage tank was filled with seawater filtered using Filter Pure polypropylene spun melt (0.5 μm pore size) and ultraviolet sterilized with an Aquastep 25 W Ultraviolet Sterilizer. The pH of the seawater in the 150 l storage tank was increased to pHT 8.45 using NaOH additions. This was necessary because the pH of seawater from the seawater collection site was 8.05, but seawater with a higher pH was needed to achieve the daytime pH values in the fluctuating mean pH 8.05 treatment (pHT 8.45). All other treatments were subsequently achieved by reducing the pH using the methods detailed below. This system was housed in a walk-in temperature controlled room at 10.8°C and under a mean irradiance of 18 μmol m⁻² s⁻¹ photon flux density 12 L:12 D ratio.

Each of the 24 A. corymbosa assemblages was cultured separately in a 650 ml Perspex flow-through culture chamber. Each chamber was attached to the outflow of an individual 1 l Perspex header tank. The pH in each header tank was controlled by automatically refilling the tank with seawater from a 1 l mixing tank. Target pHT levels were achieved in the mixing tank by adding exactly equal amounts of HCl and NaHCO₃ (a process chemically identical to adding CO₂) [26] to 1 l of seawater that was pumped from the 150 l storage tank. Before the newly mixed seawater was transferred to the appropriate header tank, pHT was measured at 10.8°C using the automated spectrophotometric system. If the measured pH was within 0.03 units of the target pHT, the seawater was transferred to the appropriate 1 l header tank. If the pH varied more than 0.03 pH units from the target value, the seawater in the mixing tank was sent to waste and the process repeated until the correct pH was achieved. Using this method, the automated system delivered new seawater at the target pH to each of the 24 header tanks approximately every 4.4 h. The order in which the seawater was refreshed in each of the 24 treatment chambers was randomly allocated at the beginning to avoid potential artefacts.

Arthrocardia corymbosa assemblages were individually tied with nylon to circular Perspex plates, each of which had six holes (1 cm diameter) to allow seawater to flow around the macroalgae. These plates were located 5 mm above the bottom of the culture tank. To minimize the thickness of diffusion boundary layers that can form at the surface of macroalgae and cause large differences in pH between an organism’s surface and the bulk
standards on an Agilent 7500ce ICP-MS using a helium collision cell Savillex vessels. The analytes were quantified against multi-element standards.

Richie [30] using ethanol extraction for chlorophyll (Chl) following the exact methods of Sampath-Wiley & Neefus [29] on day 1 and for each experimental macroalga on day 40. A Presens 50 μm oxygen microelectrode measured linear changes in oxygen concentrations over time through a purpose-built aperture. Seawater flow into and out of the cell was halted for 5 min, while oxygen evolution or consumption was recorded. Gross photosynthetic rates were calculated using linear regression then standardized to algal wet weight, and net rates were determined by deducting respiration. Algat wet weight after day 1 and before day 40 was estimated using a linear regression between the two time points for the purposes of the calculations.

The ratio of variable (Fv) to maximal (Fm) quantum yield of photosystem II (Fv/Fm) of all mature, experimental A. corymbosa was measured on days 1 and 40 using a Pulse Amplitude Modulated (PAM) chlorophyll fluorescence meter (Diving PAM, Walz, Germany). Fv/Fm was measured on A. corymbosa individuals that had been dark adapted for 15 min. This model PAM has a red-light-emitting diode, and both gain and dampening were set to 2. On all occasions, Fv was greater than 130 before measurements were made.

Pigment concentrations were determined for the six initial individuals of A. corymbosa on day 1 and for each experimental macroalga on day 40 following the exact methods of Sampath-Wiley & Neefus [29] for phycobilins (phycocyanin, PC and phycoerythrin, PE), and Richie [30] using ethanol extraction for chlorophyll (Chl) a.

%C, %N, δ13C and δ15N were analysed from the organic tissue of the initial and experimental macroalgae by removing all inorganic tissue in 1 M HCl then drying at 80°C and grinding samples in a mortar and pestle. Sub-samples were then combusted in a CE NA1500 Elemental Analyzer (Carlo-Erba instruments) interfaced to a Europa Scientific 20–20 update continuous flow mass spectrometer. Corrections for drift were made automatically every five samples from an EDTA standard with a known isotope ratio. Inorganic δ13C was also sampled in the same way, but the organic tissue was first removed with bleach [31]. The initial and treatment A. corymbosa were also analysed for Ca, Mg, Sr and Mn content. Dried samples were dissolved in concentrated HNO3 in Savillex vessels. The analytes were quantified against multi-element standards on an Agilent 7500ce ICP-MS using a helium collision cell following the manufacturer’s recommendations.

(e) Statistical analyses

Relative growth rates, recruitment, pigments (PE, PC and Chl a) and %Ca, %Mg, %MgCO3, %C, %N, δ13C and δ15N were analysed using a two-way analysis of variance (ANOVA) with pH mean and pH variability classed as factors in the model, each with two levels (pH 8.05, pH 7.65; and static, fluctuating, respectively). The interaction between the two factors was also included in the model. Fv/Fm was analysed as a repeated measures ANOVA, with time as the random factor and pH mean and pH variability as the fixed factors along with the interaction terms. Photosynthetic rates were analysed in the same way. All data used in univariate analyses were analysed for homoscedasticity and normality. Recruitment data failed this assumption and were log (X + 1) transformed. When p-values under 0.05 were detected, Tukey honestly significant difference (HSD) post hoc tests were used to determine differences between treatments. All statistical analyses were performed in R v. 2.7.0 [32].

3. Results

(a) In situ and experimental pH

pH variability within the M. pyrifera kelp bed ranged by 0.94 units (7.92–8.86) over 5 days in the austral summer (figure 1). The average pH within the kelp bed was highest in the summer (8.43), lowest in the winter (7.93) and was 8.32 on average. Clear diurnal fluctuations in kelp bed pH were evident with values decreasing at night and increasing to a peak around noon (figures 1 and 2). pH within the culture tanks that housed A. corymbosa were close (within 0.05 units) to the target pH means (means and standard error shown in table 1, for a visualization, see figure 2a,b) during the night and the day. These values corresponded to pCO2 concentrations of 145 μatm for pH 8.45, 415 μatm for pH 8.05, 1130–1150 μatm for pH 7.65 and 2960 μatm for pH 7.25. As expected, AT remained relatively constant across pH treatments. For other carbonate parameters, see table 1.

(b) Effects of pH on growth rates

Decreasing the mean pH and increasing the variability in pH both resulted in reduced growth rates for A. corymbosa over the 40 day experiment (pH mean and pH variability classed as factors in the model, each with two levels (pH 8.05, pH 7.65; and static, fluctuating, respectively). The interaction between the two factors was also included in the model. Fv/Fm was analysed as a repeated measures ANOVA, with time as the random factor and pH mean and pH variability as the fixed factors along with the interaction terms. Photosynthetic rates were analysed in the same way. All data used in univariate analyses were analysed for homoscedasticity and normality. Recruitment data failed this assumption and were log (X + 1) transformed. When p-values under 0.05 were detected, Tukey honestly significant difference (HSD) post hoc tests were used to determine differences between treatments. All statistical analyses were performed in R v. 2.7.0 [32].
with macroalgae in the pH 8.05 static treatment, growth rates were 62% lower in the pH 7.65 static treatment, 64% lower in the pH 8.05 fluctuating treatment and 98% lower in the pH 7.65 fluctuating treatment. There was no interaction between the effects of daily fluctuations in pH and the mean pH levels used ($F_{1,20} = 0.50, p = 0.49$; figure 3a).

(c) Recruitment of juvenile coralline algae

Juveniles recruited onto the Perspex plates beneath the adults throughout the experiment, and at day 40 the number of visible recruits was counted. There were between 10 and 20 recruits cm$^{-2}$ and mean pH treatment, level of pH variability, and the interaction between the two factors did not influence the number of recruits (figure 3b; $F_{1,20} < 0.21, p > 0.65$ on all occasions).

(d) Effects of pH on other biotic responses

There was no effect of decreased mean pH or increased variability in pH on rates of photosynthesis, $F_{v} / F_{m}$ pigment concentrations, nor any other measured physiological response of *A. corymbosa*. Net photosynthetic rates were not different between treatments at any given time point, nor was there any difference among treatments over time (Tukey’s HSD all $p > 0.11$; table 2). Mean $F_{v} / F_{m}$ was greater than 0.57 (indicative of photosynthetically healthy coralline algae) [34] both before and after the 40 day experiment in all treatments (see electronic supplementary material, table S1). Inorganic material accounted for 59–64% of the total dry weight and there was no effect of mean pH, the level of pH variability or the interaction between the two factors on the %Ca ($F_{1,20} < 0.48, p > 0.50$), %Mg ($F_{1,20} < 0.26, p > 0.62$), the %MgCO$_3$ ($F_{1,18} < 3.93, p > 0.06$) nor in the inorganic $\delta^{13}$C between treatments ($F_{1,20} < 2.04 p > 0.17$) (see electronic supplementary material, table S2). Pigment concentrations, C : N ratio, and the $\delta^{15}$N of the organic tissue did not vary with mean pH treatment, nor the level of pH variability ($p > 0.18$ on all occasions, see electronic supplementary material, tables S3 and S4). There was a statistically significant decrease (2%) in organic $\delta^{13}$C signatures between pH 8.05 and 7.65 treatments (see electronic supplementary material, table S4).

4. Discussion

This study demonstrates that diurnal variability in pH, similar to that occurring within coastal systems, is an important factor controlling the growth rates of calcifying organisms in today’s ocean and may have significant implications for predicting the responses of coastal calcifiers to OA. Coralline macroalgae grown in seawater with diurnally fluctuating pH (with pH higher during the day and lower at night) had significantly lower growth rates than the equivalent treatments with constant pH. The response of coralline macroalgae to OA under the fluctuating treatment was stronger than would be predicted under static conditions alone, as the absolute growth rates were even further reduced by the additive negative effects of diurnal fluctuations in pH. In addition, no other diagnostic that provides a measure of organism fitness was influenced by pH treatment, except organic $\delta^{13}$C, which increased under both lower mean pH treatments, indicating an increase in the use of diffusive CO$_2$ [35,36]. Increased variability in pH did not act to ameliorate the longer term effects of OA (at least over 40 days) as was hypothesized, but amplified OA’s negative influence on growth. This reduction in growth was most probably owing to dissolution of calcareous structures during exposure to low pH during the night (discussed below).

The response of *A. corymbosa* in this study indicates that exposure to the extremes of naturally fluctuating pH is potentially as important as mean decreases in pH owing to OA. The negative response of *A. corymbosa* to fluctuating pH is opposite to our initial predictions, and different to the response of coral recruits to fluctuations in pH [20]. The growth rate of *Seriatopora caliendra* recruits over 3–6 days was higher under a diurnally fluctuating pH treatment (pH 8.00 during the day and pH 7.77 at night) and a static low pH of 7.77, compared with a static pH 8.00 treatment [20]. Differential responses of marine organisms to diurnal fluctuations in other environmental factors have also been reported. For example, some adult corals (*Pocillopora meandrina* and *Porites rus*) respond negatively to fluctuations in temperature [37], whereas the adult corals *Pocillopora damicornis* and *Seriatopora hystrix* showed no response to fluctuating temperature, but their larvae responded positively [18,37]. Taken together, these studies indicate that responses to short-term
changes in environmental variables can be complex and the direction and magnitude of these effects may be species- (or even life-stage) specific. Short-term local variability in environmental factors driven by natural processes, such as the diurnal fluctuations in primary production highlighted in our study, may play a more important role than the long-term global changes predicted to occur owing to anthropogenic processes [38].

*Arthrocardia corymbosa* showed little response to the effects of OA compared with the responses of tropical and subtropical coralline macroalgae, where static low pH had an adverse effect on coralline macroalgal pigments, photosynthetic rates [39,40] and recruitment [41,42]. The lack of negative physiological responses to pH shown here (apart from growth) could be owing to the lower temperature (10.8°C) employed in our experiment compared with other studies. Higher temperatures exacerbate the negative impacts of OA [39,43], and experiments where widespread bleaching (i.e. mortality) or lower recruitment are reported were conducted at temperatures more than or equal to 19°C [39,41,43,44]. Another explanation for the lack of physiological responses observed in this study is that the negative responses attributed to OA by previous research could be an artefact of inappropriate methods of pH manipulation (e.g. HCl [26]), or inappropriate control of pH (i.e. high pH variability and/or no measurement of pH within the culture tank) [40,41]. Measured pH within culture tanks can be very different to that of the inflowing seawater encountered by experimental macroalgae, as photosynthesis and respiration can alter pH both within the mainstream seawater in culture tanks [45,46] and within the diffusion boundary layer around macroalgae [8,15]. We recommend that studies need to measure pH within culture tanks, provide adequate mixing/exchange of seawater and report these details sufficiently.

An alternate explanation of the lack of physiological responses of *A. corymbosa*—and potentially other species inhabiting similar coastal habitats [47,48]—to OA is that they may be tolerant of the effects of changes in pH because they regularly encounter daily shifts in pH in the field. Populations of organisms that contend with regular fluctuations in an environmental variable are often more able to adapt to permanent changes in that variable [49], owing to increased retention of phenotypic plasticity that is sometimes lost by organisms residing in relatively static environmental conditions [50,51]. By regularly encountering variable pH conditions, organisms from coastal systems may be more tolerant to the effects of continual periods of low pH caused by OA [15,52].

Our *in situ* pH measurements indicate that metabolic activity not only causes increased variability in pH within kelp forest habitats, but it may also lead to an increase in the mean pH and a decrease in the mean pCO₂ during periods of high light and primary productivity (i.e. summer). Our pH treatment of 8.05 was selected to represent the current mean pH of the world’s oceans, as recommended by the best practices guide; in future experiments, a mean pH which is representative of that within kelp beds could be used (e.g. with a higher mean pH). Furthermore, while the fluctuations in pH used here more accurately mimicked the largest amplitude of pH change occurring in the field (±0.89 units over 24 h) than in previous studies, in a future high CO₂ ocean, the night-time reductions in pH owing to respiration may be less than that used here.

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**Table 1.** Carbonate parameters (mean ± s.e.) during the day and night in the 650 ml culture tanks containing individuals of *A. corymbosa* in each of the four pH treatments. AT was measured in water taken from the culture tank (n = 48) and culture tank (n = 528). Remaining parameters were calculated from pH and AT from the culture tank at a temperature of 10.8°C and salinity of 34.3 using the Mehrbach equilibrium constants as refit by Dickson & Millero [33]. S indicates static pH treatments, while F indicates fluctuating pH treatments.

| pH     | Day     | Night   | pH      | Day     | Night   | pH      | Day     | Night   | pH      | Day     | Night   | pH      | Day     | Night   | pH      | Day     | Night   | pH      | Day     | Night   | pH      | Day     | Night   | pH      | Day     | Night   | pH      | Day     | Night   | pH      | Day     | Night   |
|--------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|
| 8.05   | 2170.2  | 2372.1  | 8.05    | 3301.2  | 3295.2  | 8.05    | 3319.2  | 3318.2  | 8.05    | 3328.2  | 3327.2  | 8.05    | 3337.2  | 3336.2  | 8.05    | 3346.2  | 3345.2  | 8.05    | 3355.2  | 3354.2  | 8.05    | 3364.2  | 3363.2  | 8.05    | 3373.2  | 3372.2  | 8.05    | 3382.2  | 3381.2  |
| 8.04   | 2168.1  | 2374.1  | 8.04    | 3299.2  | 3293.2  | 8.04    | 3317.2  | 3316.2  | 8.04    | 3326.2  | 3325.2  | 8.04    | 3335.2  | 3334.2  | 8.04    | 3344.2  | 3343.2  | 8.04    | 3353.2  | 3352.2  | 8.04    | 3362.2  | 3361.2  | 8.04    | 3371.2  | 3370.2  | 8.04    | 3380.2  | 3379.2  |
| 8.00   | 2175.1  | 2380.1  | 8.00    | 3308.2  | 3302.2  | 8.00    | 3326.2  | 3325.2  | 8.00    | 3335.2  | 3334.2  | 8.00    | 3344.2  | 3343.2  | 8.00    | 3353.2  | 3352.2  | 8.00    | 3362.2  | 3361.2  | 8.00    | 3371.2  | 3370.2  | 8.00    | 3380.2  | 3379.2  | 8.00    | 3389.2  | 3388.2  |
| 7.65   | 2182.1  | 2385.1  | 7.65    | 3317.2  | 3311.2  | 7.65    | 3335.2  | 3334.2  | 7.65    | 3344.2  | 3343.2  | 7.65    | 3353.2  | 3352.2  | 7.65    | 3362.2  | 3361.2  | 7.65    | 3371.2  | 3370.2  | 7.65    | 3380.2  | 3379.2  | 7.65    | 3389.2  | 3388.2  | 7.65    | 3398.2  | 3397.2  |

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**References:**
- [Dickson & Millero, 33]
- [Mehrbach, 8,15]
- [Arthrocardia corymbosa, 26,40,41]
- [pH measurements, 24,25]
- [Carbonate parameters, 26,40,41]
indicates fluctuating pH treatments.

iments. This will be achieved by allowing ecologically to high/low pH, this approach will be refined in future exper-

in the magnitude of pH change, and the duration of exposure will be strengthened if they acknowledge that natural varia-

ly can play in an organism’s response to OA illustrates that

of species is important for future research. While this

of pH change will influence marine organisms, we need to first

change will influence marine organisms, we need to first

realistic assemblages of macroalgae to alter pH within the

field. To make accurate predictions regarding how climate

changes owing to OA.

Further investigations examining the role that OA

will play in influencing ecological and physiological processes

will be strengthened if they acknowledge that natural vari-

ability in pH (both within the habitat and at the surface of

the organism, i.e. within the boundary layer) could influence

these processes to the same extent as OA. The variability in

pH at our coastal site is an order of magnitude larger than

recorded at open ocean sites where pH varied by 0.025

units over 13 years [23]. This is consistent with pH

measurements made in other coastal environments globally

(pH 7.25). Measurements of pH at the surface of macroalgae

indicate that respiration-driven reductions in pH in the dark

are lower in seawater simulating an OA scenario (approx.

0.10 units) than they are in ambient seawater (approx.

0.25–0.50 units), most probably because more CO2 is

needed to further lower pH as the concentrations increase

[8]. This means that future pH fluctuations encountered by

macroalgae may not be symmetrical around the daily

mean, as in the treatments used here, and that macroalgal

metabolism is even more likely to raise mean pH during

periods of high irradiance under a future OA scenario. The

investigation of these phenomena was outside the scope of

this study, but could be an important focus for future inves-

tigations examining the buffering capacity of biologically

active coastal ecosystems against pH change owing to OA.

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References


